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EVOLUTIONARY TRANSITIONS AND CO-EVOLUTIONARY DYNAMICS IN BIOLOGY AND IN CULTURE

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***Abstract**: This paper presents a Darwinian framework to study culture that formalises interactions between public and private, ontogenetic and phylogenetic as well as individual and social aspects of cultural evolution and transmission. It also compares and contrasts evolutionary milestones in the emergence of culture with major transitions in the evolution of life. We define two related processes in the evolution of culture: the cumulative encoding of innovative information into public culture and the ontogenetic development of cultural competences that allow humans to access and use that information. We claim that the capacity to create, learn and use symbols is a key factor underlying those processes.*

***Keywords**: Cultural evolution; evolutionary transition; public culture; private culture*

***Résumé**: On present un cadre Danwinien pour etudier la culture qui formalise les interactions entre des aspects de l'evolution et la transmission culturelle public et prives, ontogenetiques et phylogenetiques, individuels et sociaux. Ce cadre theoretique compares les transitions evolutives dans l'emergence de la culture avec cuus dans l'evolution biologique. On definira deux proces: la codification cumulative d'information nouvelle dans la culture publique et le developpement ontogenetique des compeetences culturelles qui nous permettent d'acceder et de se servir de cette information. Ces proces culturels sont possibles grace a la capacite de creer, aprendere et user des symbols.*

***Mots clés**: evolution culturelle; transition evoultive; culture publique; culture privee*

The aim of this paper is to present an evolutionary framework for culture informed by the elements and mechanisms of selection dynamics in biology. Natural selection was initially and mainly formulated to explain the evolution of biological species (Darwin 1859), and its application to cultural phenomena was realised by Darwin himself (Darwin 1871). Evolutionary frameworks for culture have been proposed in several fields (Dawkins 1976; Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Dennett 1995; Mace et al. 2005; Croft 2000; Mufwene 2001; Brighton, Smith and Kirby 2005; Schumpeter 1934; Nelson and Winter 1982). The remainder of this section offers an overview of evolution. Then we focus on biology, particularly on the evolutionary transition that gave rise to Darwinian dynamics and the phylogenetic tree of life. The main section of the paper analyzes a similar transition that led to co-evolutionary dynamics within culture. Specifically, we describe two levels of cultural selection, one related to function, where meanings evolve, and another related to form, where the public culture evolves. The final sections highlight the differences and similarities between evolution in biology and in culture by focusing on information flows and on causality in selection dynamics and present some implications of our co-evolutionary framework for the study of culture.

Evolution is a process whereby inheritable features arise and spread in populations. It may happen by random, undirected drift, but the focus of this paper is evolution by selection. Hull (2001) defines selection as "repeated cycles of replication, variation and environmental interaction so structured that environmental interaction causes replication to be differential". In selection systems, "like begets like", but interaction with the environment yields "descent with modification" so that over the generations, the information in a population reflects the structure of its environment. The following paragraphs define and illustrate the elements (the unit of replication and the vehicle) and processes (replication, variation and adaptation) of selection. Fig.13.1. illustrates a selection system.

Hull (1988) defined the unit of replication as "the entity that passes on its structure largely intact in successive generations". Dawkins (1976) emphasized the role of genes as entities that contain the information that is passed on during replication, but we follow Williams' (1992) view that the unit of replication is defined by its information content. Information can be defined for our purposes as any pattern that influences the formation or the transformation of other patterns. Several units of replication have been proposed in culture: in the economy, routines and rules (Nelson and Winter 1982); in the evolution of science, beliefs, goals and methodologies (Hull 1988); in linguistics, structural linguistic features (Croft 2000, Mufwene 2001, Tamariz 2006).

A second element of Hull's (1988) general account of selection is "the entity that interacts as a cohesive whole with its environment". Dawkins (1976) called this the "vehicle". In biology, the vehicle is the phenotype that develops when the genetic information unfolds in an environment. In the economy, Knudsen and Hodgson (2004) propose that firms are vehicles for the replication of habits and routines. In Hull's (1988) evolution of scientific knowledge, the vehicles are the scientists. In some linguistic models, vehicles are the speaker and his grammar (Croft 2000, Mufwene 2001, Tamariz 2006).

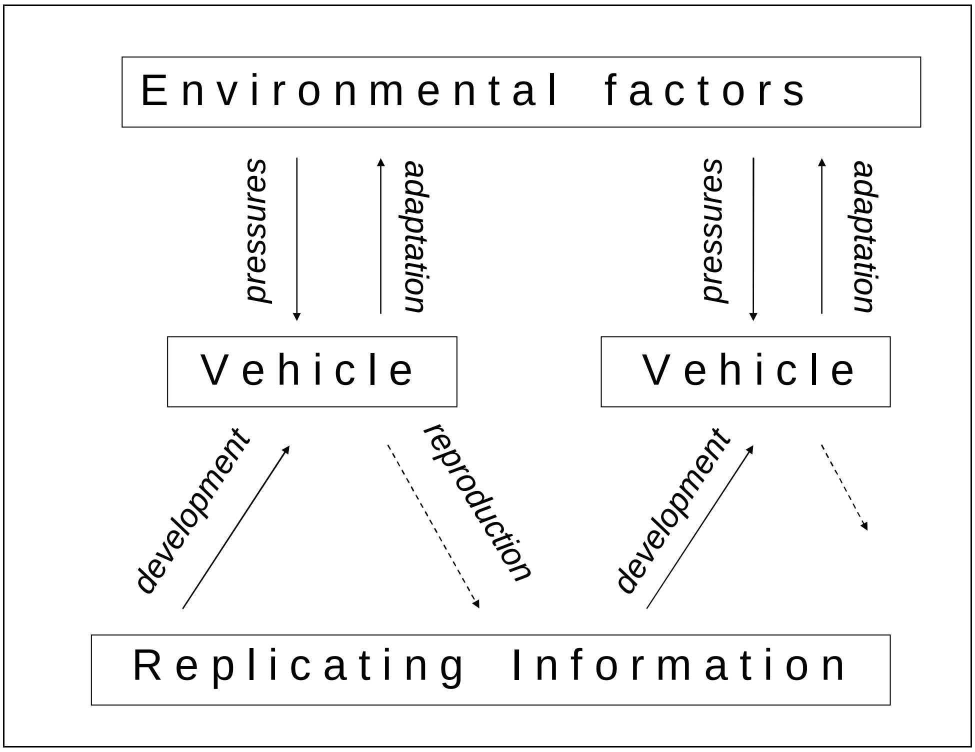

Fig. 13.1. The elements of a Darwinian selection system

Replication is related to copying information. Three criteria define replication in an evolutionary system: causation, similarity and information transfer between original and copy (Hodgson and Knudsen *in press*).

Selection can only occur if there exist inheritable variants of the units of replication with different fitness values. Variation may originate in mutation (a change to the replicating information) and in recombination.

Any non-replicating information that contributes to the self-sustainment of an evolutionary system is considered to be environmental information. Metaphorically speaking, the environmental information constitutes the fitness landscape where replicating information evolves. In that way the environment constrains the possible evolutionary histories of a system, resulting in adaptation. Selection is the process whereby the path of a complex system's evolution is carved in that landscape.

MOLECULAR EVOLUTION

Cyclical chemical reactions are at the heart of a widely accepted hypothesis to explain the origin of life, namely autonomous replication, or "continued growth and division which is reliant on input of small molecules and energy only" (Szostak *et al.* 2001). Primeval life systems present a unit of replication (information about the structure of self-replicating units) and a vehicle (the molecules themselves), and encompass variation, replication and environmental interaction. The inheritance of features of the molecules is both caused by the replicating information and by the stability of the environment (first the primeval soup and later the intracellular environment, whose homeostasis is tightly regulated and constitutes the first "niche" that self-replicating molecules constructed around themselves and transmitted non-genetically over the lineages). Replication occurs because there is causation, similarity and information transfer when the system keeps producing more of the same networks of molecules. Variation is brought about by random changes in the structure of the component molecules and by recombination of existing ones through horizontal transfer of information. Adaptation results from the inherent interaction between the molecules and their environment.

Apart from horizontal information transfer, early life systems diverge from organismal selection in that they do not include translation mechanisms and therefore the information they contain is only about their own structure (strongly constrained by the adaptive pressure posed by the function of self-replication). In other words, the vehicle is also the repository of the information and consequently, the processes of replication and ontogeny (development) are one and the same.

ORGANISMAL EVOLUTION

Woese (1998) identifies the origin of cells able to translate nucleic acids (DNA, RNA) into proteins as the most important single event in evolutionary history and as one of the great transitions in evolution that are characterized by the appearance of new ways of transmitting information (Maynard Smith and Szathmáry 1995) or by new mechanisms of symbolic representation (Woese 2002). The transition at hand, termed the Darwinian Threshold by Woese, occurred when horizontal transfer of replicating material led to complex cells where the mechanisms of translation evolved. If genes are defined as the stretch of DNA that code for the amino-acid sequence of a protein, then the onset of translation from nucleotide sequences to proteins effectively brought about a new unit of information: the gene. Woese (1998) points out that, with translation in place, vertical transfer of genetic information leads to an increasingly permanent organismal genealogical trace. Speciation in the Darwinian sense begins and genetic information is now amenable to representation by a tree topology.

Replication of genes is mediated by the phenotypes. Mechanisms for variation include mutation, and recombination, which may occur by sexual reproduction or by horizontal gene transfer (the latter is illustrated e.g. by Woese 2000's report of cases of acquired antibiotic resistance in bacteria). Adaptation is observed at the level of the phenotype, with respect to its development and its ability to reproduce in an environment. The informational systematicity between genes and the environment is achieved through natural selection.

THE ORIGIN AND EVOLUTION OF CULTURE

Let us start with a definition by Mesoudi *et al.* (2004): "[Culture is] acquired information, such as knowledge, beliefs, and values, that is inherited through social learning, and expressed in behavior and artifacts". This definition points at two distinct entities: private or cognitive information residing in individual minds and public manifestations of culture expressing the private information. Mesoudi *et al.'s* definition seems to imply that culture comprises private aspects only while public culture is the expression of private culture. Similarly, for Boyd and Richerson (1985), and the memetics literature (Dawkins 1976, Dennett 1995), culture is information stored in human brains. The focus of cultural and social anthropology, on the other hand, is the material or public aspect of culture.

Back to Mesoudi *et al.* (2004)'s definition, culture is not innately or genetically specified, but socially learned during an individual's lifetime. Additionally, public culture is symbolic because the information is "about" something other than the repository of the information, and internally structured because informational entropy is not maximal, and therefore some redundancy (complexity) can be measured. Some animal communication systems share some of these characteristics: birdsong is socially learned and is internally structured but not symbolic (it does not have meaning); apes can use, learn and even categorize symbols (Savage-Rumbaugh *et al.* 1980), but cannot cope with complex syntactic structure; bee dance is symbolic and structured, but not socially learned. The only system that is mostly socially learned, symbolic and structured is human culture, the main subject of this paper. Ultimately we must not forget that culture is limited by the fact that it must, overall, increase human fitness.

CULTURAL TRANSITIONS

We distinguish three states of a population with respect to culture: in the first, there is no communication between individuals; in the second, an unstructured communication system allows transmission of meanings between individuals, and in the third, the communication system is structured. The "Cultural threshold" is positioned between the second and third.

We assume that before culture emerged, our ancestors could entertain thoughts, and that this is also the case with other primates (Hurford 2007). The repository for the replicating information in meanings or thoughts are patterns of neural activity akin to Aunger's (2002) "electric memes". These meanings were locked inside individual brains and may have been produced repeatedly, or replicated, when prompted by external or internal events. We propose that this stage is formally analogous to Woese's pre-Darwinian era in biology: some information is maintained over time (within an individual's lifetime) thanks to stable environmental input (objects and events in the world). Moreover, horizontal transfer of information between meanings within one brain may have been possible through of metaphor and analogy that would have been resulted, for instance, from the increased cognitive fluidity proposed by Mithen (1996).

A first transition occurs when meanings are encoded in a repository different from the neural substrate. The advent of communication is enabled by the evolution of a translation mechanism that allows encoding and decoding between private meanings and public forms, namely symbolic association. (Note that innate symbolic association is present in animal communication systems, but human communication is socially learned). Communication systems bring about two novelties: the replication of meanings between brains and the production of symbols, (public behaviours and artefacts that express meanings), both of which play a crucial role in the emergence of culture.

The transition to culture is marked by the advent of a new cognitive capacity to create and learn new symbolic associations between patterns observed in public culture (which is symbolic itself) and existing or new meanings. This capacity generates a process of structuring, complexification or organization (i.e. evolution) of public forms over time. We can define a second translation process that induces the emergence of a new kind of

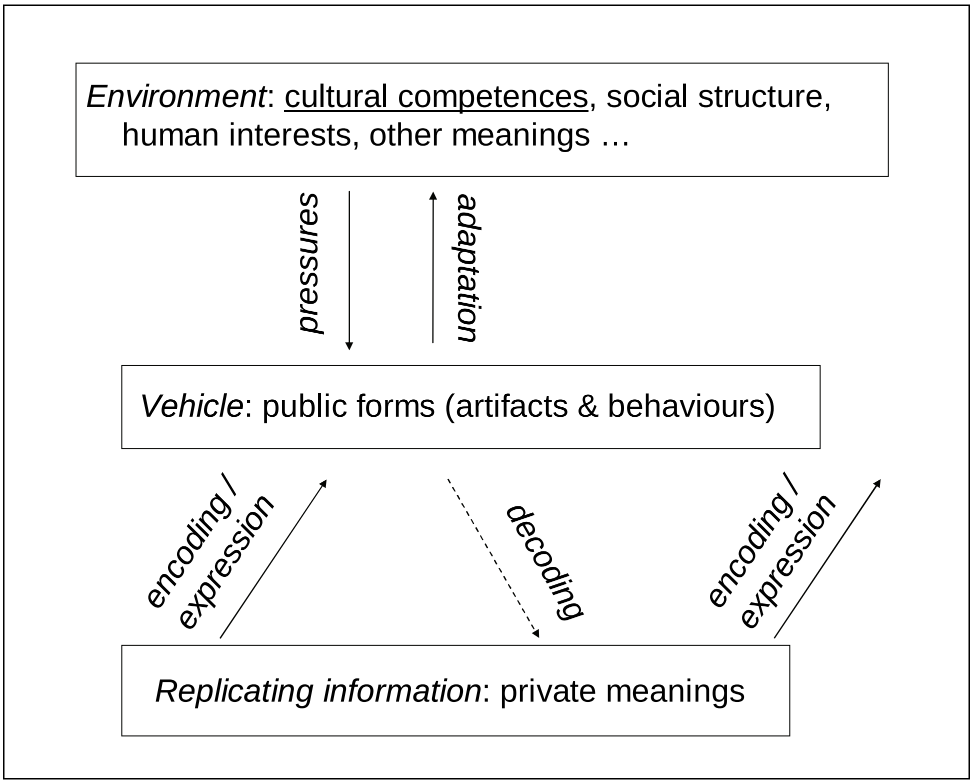

Fig. 13.2. Elements and mechanisms of selection of public forms

information. In a communication system, the sturcutre of public forms is in principle irrelevant (as long as they can be perceived as distinct from each other). We claim that, in a cultural system, an innate, human-specific ability to detect patterns in the structure of public forms and, crucially, to convert those patterns into symbols by assigning them meanings (non-innately) makes the structure of public forms relevant. The new ability results in the ontogenetic development in the brain of each member of a society of a collection of symbolic associations between meanings and forms. We call these mental entities cultural competences, because they allow individuals to encode and decode, to access and to use the information in public culture. These novelties dramatically transform the communication system by making it cumulative. Meanings transcend the spatio-temporal limits of individual brains and lifetimes by finding a new repository in public forms. Public forms become ever more complex because information about their own structure evolves in populations over the generations.

THE EVOLUTION OF PUBLIC FORMS: COMMUNICATION

We now describe a co-evolutionary framework encompassing public and private aspects of culture that includes two selection systems, each with its units of replication, vehicles, environmental interactions, and mechanisms of replication and variation. In a way similar to the above description of molecular and organismal selection, we will describe selection of public forms (Fig. 13.2) and of competences (Fig. 13.3).

Units of Replication and Vehicles. During communication, public forms are the vehicles that express (that are symbolically associated with) private meanings. The units of replication, meanings, are neurally encoded and, therefore, private.

Replication. Replication happens during communication when a copy or a person's private meaning is produced in another person's brain.

Variation. Variation of meanings can originate in horizontal transfer, or recombination, of information among the meanings residing in the same brain during metaphorical and analogical activity.

Adaptation. Several environmental factors configure the fitness landscape where meanings evolve. First, cultural competences, the conventionalized mappings that allow encoding and decoding between meanings on the one hand and cultural behaviours and artefacts on the other hand, which are explained in detail in the next section. Second, innate biases related to human fitness determine the extent to which different meanings are expressed and attended to by making individuals devote preferential attention, time and resources to certain aspects of the environment, such as the social structure, mating or food. Third, the social structure bears on the fitness of meaning, as it affects the opportunities for communication between

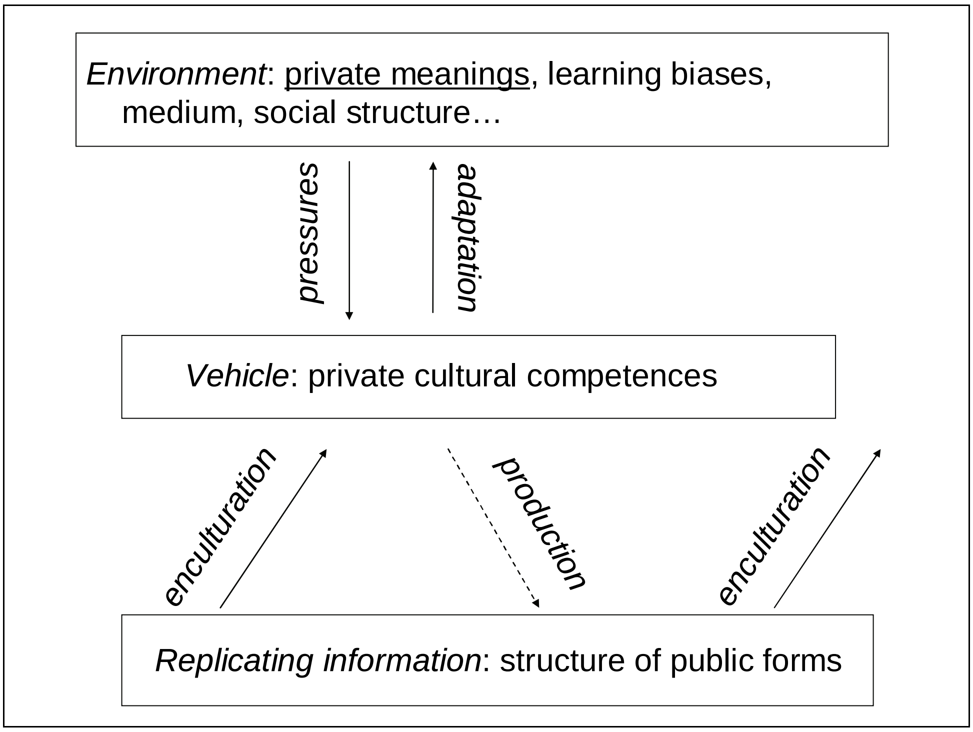

Fig. 13.3. Elements and mechanisms of selection of cultural competences

people. Fourth, other meanings in recipient brains interact with existing meanings, affecting their fitness.

THE EVOLUTION OF COMPETENCES: CULTURE

As we saw above, the transition to organismal evolution in biology took place when translation between nucleic acid strings and proteins became available and brought about a new kind of symbolic information (genetic information). In culture, translation between private meaning and public form brought about the possibility of communication. The cultural threshold (second transitions) was crossed when a new encoding of information emerged. When humans (genetically) evolved the capacity to learn symbolic associations between private meanings and patterns in public culture, competences, or sets of associations between inferred meanings and observed patterns in public culture, began to develop in our brains thanks to exposure to and use of culture. Fig. 13.3 illustrates the resulting selection system.

Units of Replication and Vehicles. Our account of the emergence of culture entails the appearance of a new kind of replicating information: the regularities detected in the structure of public artefacts and behaviours. This new information is symbolically associated to aspects of the meanings that the public forms convey, for instance, the occurrence of "–ed" in English speech is inferred to be associated with past tense. The vehicles for the replication of the new information are (private) human cultural linguistic, social, technological or economic competences, the codes that develop during enculturation, for instance, through disambiguation across multiple contexts (Smith 2005).

Replication. The replication of structural features of public forms occurs when an individual produces cultural output that has the same structure as the cultural input which contributed to his or her enculturation. For instance, when a person speaks, their output speech has the same structure (phonology, syntax) as the language that elicited the development of her linguistic competence.

Variation. Variation in the pool of public culture features may originate in imperfect replication (mutation) and in recombination (e.g. combination of form feature information from different sources during enculturation).

Adaptation. The environmental factors that determine the fitness of the replicating information about the structure of public forms include the social structure and innate learning biases such as the human capacity to learn from repeated exposures (Smith 2005), the ability to participate in social interaction involving shared attention (Tomasello 2003) and the capacity to create and manipulate new symbolic associations between patterns inferred from public culture and new meanings, that is, to turn public culture information into symbols (Deacon 1997).

CO-EVOLUTIONARY INTERACTIONS IN CULTURE

We have proposed that there are two evolutionary systems in culture. The first is concerned with the transmission of private meanings between brains by means of cultural forms during individual acts of communication. The second is concerned with the transmission of the structure of public forms over the generations by means of competences. The two are intimately connected: the development of cultural competences (enculturation) is a prolonged process involving repeated single interactions in which meanings are encoded into and decoded from public forms. We now describe three interactions that characterise their co-evolution. First, competences are needed for the replication of meanings, i.e. for encoding and decoding between private meanings and public cultural forms. Second, private meanings are needed for the development of competences: This development involves establishing symbolic mappings between structural features of forms and aspects of meanings. Third, conversely, the extraction of structural patterns from public culture may result in the creation of new meanings, as patterns that are noticed may be associated with a consistently co-occurring meaning. Fourth, public forms as vehicles for meanings are the repositories for the replicating information of the system of competences (structural features of public forms).

EVOLUTION OF LIFE, EVOLUTION OF CULTURE

We have now a detailed account of two selection systems in life and in culture and are in a position to compare and see interactions between both. The most relevant similarity is the fact that both in culture and in biology we find two co-evolving systems, the second of which results from an evolutionary transition characterized by a mechanisms able to extract information from a structure that so far functioned as a vehicle for other information patterns.

The co-evolutionary relationships between genes and culture have been the subject of extensive study (e.g. Durham 1991, Cavalli-Sforza and Feldman 1981, Boyd and Richerson 1985, Lumdsen and Wilson 1981). During the evolution of our cultural niche (Odling-Smee, Laland and Feldman 2003) humans have become increasingly reliant on culture, which has deeply transformed the fitness landscape of human genes. The information (knowledge, meanings) that humans use is increasingly encoded in public cultural repositories, and correspondingly less in private neural repositories. Natural selection's adaptation to this shift is a neural environment capable of translating between private meanings and public forms. Public culture has thus relieved the human brain of the pressure to store large amounts of information. With less pressure to encode meanings privately, neural resources can be devoted to competences, the interface between currently relevant meanings and public culture. For example, the invention of writing relieved storytellers from the need to carry the stories in their heads, but required them to learn to read. Cultural evolution has entailed a process of downloading information from brains onto public culture, while brains have adapted to house interfaces that help us access and use parts of the information encoded in culture efficiently and only as required. For a new competence to be evolutionarily stable, the amount of information it makes available (by accessing it from public culture) must be greater than the amount of "memory space" it takes in the brain, or the information it could hold in the same amount of neural resources.

One important difference between culture and biology concerns reproduction. In culture, the structural public culture information that recombines in each new individual competence does not come from two parents, as in biological sexual reproduction, but from a multitude of other individuals. Indeed, we can learn from older, younger and contemporary individuals. This might preclude the existence of traceable lineages of public cultural information; however, because of the asymmetrical learning between human generations (i.e. children tend to learn from parents more than vice versa), information transmission in the system of competences such lineages become traceable. This is related to another departure of the form selection system from the paradigmatic case of organismal natural selection. In sexual organisms, fertilization is the process whereby genetic material (information) from an egg and a sperm fuse to form a new genotype. In cultural competences, gathering replicating information is an extended process that continues throughout an individual's lifetime. Learning during enculturation is incremental, which means that the patterns learnt by one individual become more robust as he is exposed to more exemplars. Early exposures have a greater impact on the development of competences and later exposures have decreasing impact, contributing to a flow of information down the human generations where younger individuals are net recipients and older individuals are net contributors. This unidirectional net flow of information results in a mostly vertical transmission that underlies a stable genealogy of the information about the structure of public cultural forms.

PREDICTIONS AND EXTENSIONS OF THE CO-EVOLUTIONARY FRAMEWORK

The co-evolutionary dynamics for culture we have described produces predictions that could be tested empirically or with computer simulations concerning the origin, workings and evolution of cultural systems.

The complexity of an evolving system increases over time through an accumulation of frozen accidents (Gell-Mann 1994). One prediction stemming from this fact is that increased complexity in the two proposed co-evolving systems should boost each other's complexity in three ways: first, unintended information may be extracted from the cultural environment, leading to complexification over the generations of cultural competences; second, more complex competences may encode and decode more complex meanings into forms; third, more complex forms may contain more complex structural information and fourth, more complex meanings pose pressure for more complex vehicles to encode them. This hypothesis has been successfully tested with a computer model (Tamariz and Vogt, in preparation); further evidence could be gathered from examining the rate and timing of change of private and public culture in various domains, such as archaeology, the economy, technology, anthropology or linguistics. Moreover, the synergistic complexification of culture may have posed a pressure for the complexification of the neural substrate.

The co-evolutionary framework can be applied at other levels of analysis within culture, which can be illustrated with an example from information technology: the evolution of information contained in computer files and in the software and hardware used to transmit that information. Evolutionary transitions in culture happen when new repositories of information become available and new competences evolve to access and use the information in the new repositories. The equivalent evolutionary transitions in IT happen when new ways of storing information are used (e.g. files used to be stored in individual computers, now they can be stored on the Internet, disks etc.) and new ways to access and use that information emerge (e.g. increased processing power to compress and decompress files, increased connectivity and bandwidth to upload and download them from the new repository). In each such transition the pressure on earlier storage devices is eased: we saw earlier how the advent of the printed word relieved individuals from the pressure to commit information to memory; similarly, the Internet may store vast amounts of information that would not fit into a single computer. The process that co-evolves with this is an ever-increasing complexification of the cognitive competences and the technologies that allow people and computers, respectively, to encode information onto public domains and download it as required, which is, effectively, what humans do in our lives as cultural beings (see Clark 2003). This trend, in turn, poses a pressure towards the complexification of the substrate for those competences, be they neural or computer hardware, which is attested by the evolution of the human brain and of the communication apparatus and of information technology.

CONCLUSION

A parallel account of the evolutionary dynamics of culture and biology has revealed that despite obvious differences, fundamental similarities can be observed between the two. Furthermore, these general principles may be applicable to other domains. These commonalities may be characteristic of adaptive complex systems undergoing transitions prompted by new translation mechanisms. We have made the following specific claims about cultural evolution:

The evolutionary dynamics of the systems of cultural forms and competences are analogous in some fundamental ways to molecular and organismal evolution in biology. In both cases, a transition occurs when a new kind of symbolic information previously present is processed by a translation system that ultimately leads to replication of the new information.

Culture comprises two kinds of information: neurally-encoded private meanings and information about the structure of public cultural forms. They define two selection systems that evolve at different rates through different mechanisms but nevertheless are integrated within one co-evolutionary unit, as they provide fundamental evolutionary elements and mechanisms for one another. This account of culture can be inscribed within a wider gene-culture co-evolutionary framework. Additionally, co-evolutionary dynamics can be applied to complex interactions at other levels within culture.

The result of cultural co-evolution is that private meanings can be encoded in the virtually unlimited distributed repository that is public culture. Individual cultural competences are the interfaces that allow individuals to interact with public culture environment as and when needed. As new repositories of information emerge, complexifying public culture, the competences that process that information also become increasingly complex. This in turn poses a pressure on natural selection of genetic information for the complexification of neural resources.

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